THE PANORPOID COMPLEX.

PART 2. THE WING-TRICHIATION AND ITS RELATIONSHIP TO THE GENERAL SCHEME OF VENATION.

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(Plates lxvii.-lxix., and Text-figures 17-34).

If we cut off a small portion of the wing of any archaic Holometabolous Insect, such as, for instance, *Archichauliodes guttiferus* Walk., (Text-fig.22) of the Order Megaloptera, and make a cleared mount of it, we shall find that, when it is examined under a high power, both veins and membrane of the wing are covered with hairs. These hairs will be seen to be developed equally abundantly upon the upper and under sides of the wing.

This covering of hairs may be spoken of collectively as the *Wing-trichiation.* Though it is to be found in all Orders of the Holometabola, it does not occur in all Orders of Insects. It is, for instance, entirely absent from the wings of the Odonata.

Generally speaking, there may be found upon the wing of any Holometabolous Insect two types of hairs, which I have already named microtrichia and macrotrichia respectively (**5**). These may be defined as follows:—

Microtrichia (Gr. μικρός, small; and θρίξ, τριχός, a hair) are minute hairs, generally much curved or hooked, which are developed in connection with every unspecialised hypoderm-cell of both upper and under surface of the wing. Hence they occur indiscriminately and exceedingly abundantly upon veins and membrane alike. Their bases of insertion appear as simple circular pits, in which, under a very high power, a central perforation leading into a very small lumen in the interior of the hair can be made out. They vary in length from under 1μ to about 30μ, but in most cases lie between 10μ and 20μ. Similar hairs are frequently present upon the softer parts of the body, as, for instance, on the abdominal sutures and pleuræ. (Text-fig. 17, *a*, *d*).

Macrotrichia (Gr. μακρός, large; and θρίξ) are much larger and stronger hairs, much less abundant, and only developed from large specialised hypoderm-cells (trichogen cells) in connection with special nerve-endings. They are thus of the nature of *sensillæ*, and homologous with similar hairs on other parts of the body. Their bases of insertion are in the form of raised circular rings, enclosing an opening in the cuticle, which is continued as a very definite lumen within the hair, almost to its very tip. These hairs are almost universally present upon the main veins and their branches, less frequently upon the membrane of the wing, and only in very special cases upon the true cross-veins. In several Orders they become evolved, in certain cases, by a process of flattening, into *scales*; but this development is only spasmodic except in the Order Lepidoptera, where scales are found universally. (Text-fig. 17, *b*, *c*, *e*, *f*).

Text-fig. 17.*

Those macrotrichia found upon the veins are usually somewhat larger and stronger than those found upon the membrane, and both series may vary considerably in size upon the same wing. In different insects, the limits of variation of these hairs may be placed at from 40μ to over 200μ. Text-fig. 17 shows two sets of fairly normal hairs, one from *Panorpa*, and one from *Rhyphus*.

It is the purpose of this Part to study the evolution of the Wing-Trichiation in the various Orders of the Panorpoid Complex. As this is partly dependent upon the state of evolution of

* Hairs from the wings of *Panorpa confusa* Westw., (*a-c*), and *Rhyphus brevis* Walk., (*d-f*); *a*, *d*, microtrichia; *b*, *e*, macrotrichia from wing-membrane; *c*, *f*, ditto, from main veins; (×375).

the general plan of the wing-venation, it will be necessary, first of all, to define the composition of this venation somewhat more strictly than is usual.

According to the well-known, and by now generally accepted, theory of Comstock and Needham (**14**), the venation of an insect's wing has been originally determined by the courses of the precedent tracheæ, which supply the growing wing-rudiment of the larva or nymph. From the six main tracheæ that enter the growing wing, there are thus developed six *main veins*, known as the *costa*, *subcosta*, *radius*, *media*, *cubitus* and *analis*, respectively. Some of these main veins may be branched; such primary branches are termed *sectors*.

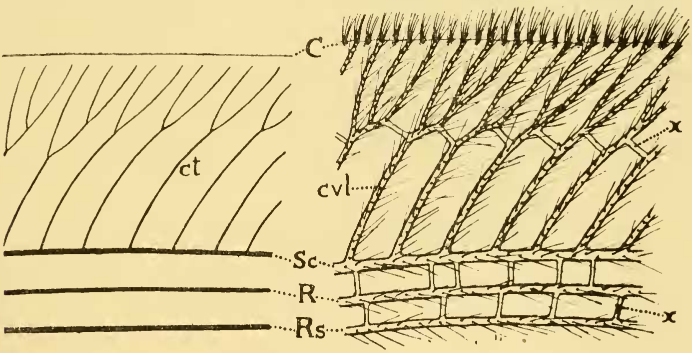
In the case of a main vein which branches and rebranches several times, it is clear that the final branchlets may be both very small and very numerous. I propose to term such branchlets *veinlets*. They are to be distinguished from cross-veins (see below) by the fact that they are always preceded by definite tracheæ.

In contradistinction to a veinlet, I propose to restrict the term *cross-vein* to a short connecting vein which does not form part of the branching system of any main vein, and is developed independently of the precedent tracheation.

It should be clearly understood that there is no reason why such true cross-veins should not be developed upon any portion of a wing, and *at any time*, provided the need for them arises. There is thus, in reality, no difference between true cross-veins and the so-called *false cross-veins*, which appear occasionally in newly-expanded areas of the wings of highly specialised genera; as, for instance, in the enlarged humeral area of the hindwing of *Lasiocampa*. The only difference between these newly formed cross-veins and those found in older wings is one of *time*; where the geological record is available to us, as in the case of the *Psychopsidæ*, the rise of the true cross-veins from a similar origin is clearly indicated.

In order to appreciate the difference between veinlets and cross-veins more clearly, I have figured the tracheation and corresponding venation of a portion of the costal area of the forewing of *Psychopsis elegans* Guérin, (Text-fig.18), in which this difference is very clearly shown. It will be seen that the branches passing into the costal area from the main subcostal vein (Sc) are all of the nature of *veinlets* (*cvl*), since they are all preceded by tracheæ. These veinlets are, however, supported by true *cross-veins* (*x*), which have arisen independently of the tracheation. Also, the narrow areas between Sc, R, and Rs are strengthened by true *cross-veins* (*x*).

In the known fossils of the *Psychopsidæ* and allies, we find the costal veinlets present as in recent forms. But there are no connecting cross-veins. Hence it is evident that these latter are a later development, called into existence by the need for strengthening the enlarged costal area of the wing.

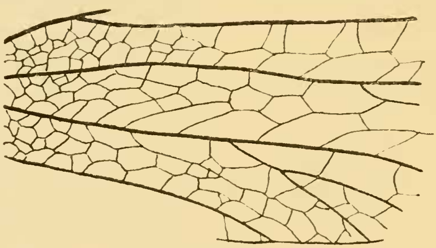


Text-fig.18.

Portion of enlarged costal area of forewing of *Psychopsis elegans* Guér., (×27), with the corresponding tracheation (to the left) of the pupal wing, (×60). C, costa; *ct*, tracheæ preceding the costal veinlets; *cvl*, costal veinlets; R, radius; Rs, radial sector; Sc, subcosta.

Referring again to Text-fig.18, we notice a further difference between the veinlets and the cross-veins. The former, like the main veins of which they are branchlets, carry a regular series of macrotrichia, whereas the latter have no macrotrichia at all. This distinction holds throughout the whole of the Holometabola, with only two exceptions, viz., the Raphidioidea and the higher families of the Planipennia, in which the macrotrichia appear upon the cross-veins as well as on the veinlets.

Having now clearly explained the difference between veinlets and cross-veins, let us now go back to the most primitive fossil insects, and study the venational scheme that they present to us. In the oldest known Orders, the Palæodictyoptera and their allies of the Upper Carboniferous, we find the same scheme of main veins as in recent insects. The spaces between these main veins and their branches are, however, filled up with an irregular meshwork of cellules, quite unlike anything to be seen in the Holometabola of to-day, though very probably homologous with the still-existing dense meshwork of cellules to be found in certain Orders of Hemimetabola, such as the Odonata. To this *original meshwork of cellules*, as developed in the Palæodictyoptera and their allies, I propose to give the name *archedictyon*. A portion of a typical archedictyon is shown in Text-fig. 19.



Text-fig. 19.
Portion of wing of the fossil *Hypermegethes shuckerti* Handl., (Order Palæodictyoptera), to show the archedictyon; (nat. size).

It is here necessary to disabuse our minds at once of the idea, if it exists, that the dense venation found in certain Planipennia is an archedictyon. Practically all known fossils of this Order (Triassic, Liassic, and Jurassic) have either no or few cross-veins, and the spaces between their numerous main veins and branches are devoid of any meshwork. Further, the oldest types still extant, such as the *Psychopsidæ*, *Ithonidæ*, etc., have no meshwork present; and it is demonstrable that the apparent meshwork present in the newer families, such as the *Myrmeleontidæ* and *Ascalaphidæ*, is to be traced back to a simpler arrangement of numerous parallel sectors supported by cross-veins at intervals. It is by the zigzagging of these sectors, and the consequent production of numerous polygonal cellules, that a meshwork appearance has been produced.

The essential characters of the original archedictyon, as we find it preserved in the Palæodictyoptera, are its irregularity, and the delicacy of the *venules* (I use this term as distinct from veinlets or cross-veins) that form it. Whether these first arose in connection with precedent fine tracheæ in the wing-rudiment, or entirely independently of them, or perhaps partly in one way and partly in the other, we have now no sure means of proving. We can only say that the irregularity of their courses, and the fact that, in one fossil at least, macrotrichia have been found to exist upon them, strongly suggest a tracheal basis.

It is now necessary to show the inter-relationship between the archedictyon proper, the veinlets and cross-veins of the wing, and the trichiation. Fortunately all these are preserved together in the fossil Order Protomecoptera, from the Trias of Ipswich, Queensland.

Plate lxvii., figs.9-10, show portions of the wing of *Archipanorpa magnifica* Till., the only known representative of this Order. Here we may see the archedictyon still complete, but evidently in a stage preparatory to becoming completely merged into the wing-membrane. The venules of the archedictyon are not definitely marked out, as in such fossils as *Hypermegethes* (Text-fig. 19), but appear rather as simple ridges of the cuticle, not showing any definite venular structure. In many places, but chiefly close to the main veins, and at the angles of the meshwork, there can be seen rounded or slightly oval tubercles, of a diameter considerably smaller than those seen upon the veins themselves, and, with few exceptions, less clearly preserved. These are evidently the bases of insertion of macrotrichia; but, partly owing to the weak development of the meshwork that carries them, and partly because they apparently lay more flatly along the wing-surface, their bases are not preserved as well as those on the veins, and very rarely show the two concentric circles which characterise the base of a stiff and more upright bristle. In my original description (5. Pl. viii., fig.6), I gave a diagrammatic figure of a small portion of the archedictyon of this fossil, much enlarged. I now consider this figure to be somewhat misleading, in that it made the macrotrichia of the meshwork appear as large and as clearly marked as those of the veins, whereas they are always smaller, and in most parts of the wing more difficult to make out. It will be readily seen from the photomicrographs that it is not an easy matter to give a correct drawing of this meshwork, and I think it better simply to give the photographs in this paper.

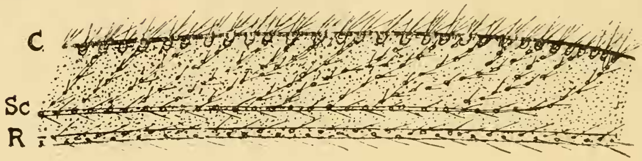
So well is this fossil preserved, that I have been able to find, in several parts of the wing, by the use of careful lighting, definite indications of the fine pitting due to the presence of microtrichia. Their bases of insertion are of about the same diameter as that of the average particle in the grain of the rock, viz., from 2 to 3μ. From a comparison with the microtrichia of *Panorpa*, we may therefore conclude that the length of these microtrichia was 40μ or more; *i.e.*, considerably larger than any to be seen in existing Holometabola.

Measurements of the beautifully preserved bases of insertion of the macrotrichia upon the main veins of this fossil show that the outer diameter of most of them lies between 30 and 40μ. This is much in excess of the size to be found in the wings of existing Orders, which seldom exceeds 10μ. Allowing some expansion due to the pressure upon the wing during fossilisation, it would still appear that this insect possessed macrotrichia very much stouter and longer than any now known to exist; their probable length was between 300 and 400μ. The macrotrichia upon the archedictyon were evidently smaller, and probably did not exceed 200μ, their bases of insertion averaging only 20μ.

The cross-veins in the fossil are clearly seen to be developed as strong struts between the main veins, and are quite independent of the archedictyon. With the exception of one or two macrotrichia that appear to have strayed on to them from the latter, they are found to be quite free from these hairs. Hence they show no evidence whatever of having been developed by straightening out of any portion of the archedictyon. If they had been so developed, it is clear that they must have carried macrotrichia, which they would receive from the archedictyon itself.

It will be seen, from the fossil *Archipanorpa*, that the macrotrichia occurred originally only upon the main veins and their branches, including the true veinlets, and upon the archedictyon. Cross-veins and membrane of the wing are alike free from them. When, however, the archedictyon is absorbed into the membrane (as it is on the point of being, in this fossil), it is evident that the macrotrichia that originally occurred upon the archedictyon must then become seated upon the membrane. This will explain their appearance upon the membrane in many Orders of Holometabola. But, if this explanation be correct, then the arrangement of the macrotrichia might be expected to show some signs of the original design of the archedictyon. If we draw the positions of a number of macrotrichia in any of the older Holometabola, we shall see that this is the case. For this, it will only be necessary to refer again to Text-fig.22, in which it will be seen that the macrotrichia below the main vein there figured tend to lie along oblique lines similar to the courses of the venules running out from the main veins in the fossil wing shown in Text-fig.19; and, like them, are connected by shorter cross-branches, indicated by the presence of macrotrichia lying in intermediate positions. (See also Text-figs. 21, 26, 30, 34).

Further evidence as to how the macrotrichia first appeared upon the membrane of the wing may be obtained by a careful study of the pterostigmatic region in the Planipennia. Text-fig. 20 shows this region in *Micromus tasmaniæ* Walk. The series of costal veinlets, that fills the costal space in all Planipennia, originally extended into the pterostigmatic region. Here there is a gradual thickening of the membrane taking place, with a correspondingly gradual absorption of the veinlets; all stages of this process can still be seen going on by studying various species in the families *Hemerobiidæ*, *Chrysopidæ*, and *Mantispidæ*. As these veinlets carry macrotrichia, it will be obvious that, as they disappear, the macrotrichia will become seated upon the membrane.



Text-fig. 20.

Pterostigmatic area of forewing of *Micromus tasmaniæ* Walk., showing aphantoneuric condition of the veinlets; (× 15). C, costa; R, radius; Sc., subcosta.

Thus we see that the evidence both of the fossil Order Protomecoptera and of the recent Planipennia agrees in pointing to the same conclusion:—*Macrotrichia were originally carried only upon the main veins and their branches, and upon the archedictyon; they appear upon the membrane by absorption of the veinlets or venules, carrying them, into the membrane of the wing.*

From this we come to the further conclusion that:—*The presence of macrotrichia upon the membrane of wings of an open-veined type (*i.e., *one which has no close meshwork of numerous veins) is to be regarded as evidence of the descent of such forms from more densely veined forms.*

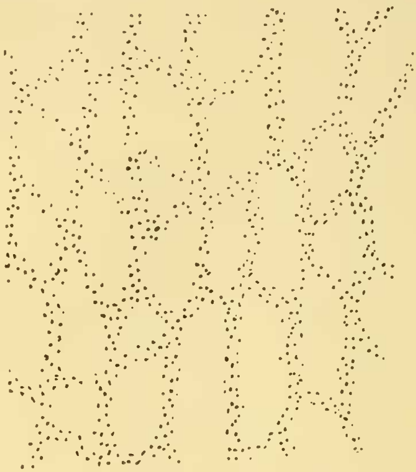
The process by which the archedictyon, or any series of veinlets, becomes merged into the membrane, may be termed *aphantoneurism*, and veins which are in process of disappearing in this manner may be called *aphantoneuric.* It is often possible to reconstruct the aphantoneuric meshwork, merely by plotting the positions of the macrotrichia upon the membrane, and joining them up into a polygonal meshwork. Text-fig. 21 shows a reconstruction of a small portion of the aphantoneuric meshwork of the Hawk-moth *Cœquosa triangularis* Don.

Having now explained how the Wing-trichiation is connected with the venation in general, we may proceed to trace out the various lines of evolution within the Orders of the Panorpoid Complex.

Order PROTOMECOPTERA. (Plate lxvii., figs.9-10).

We have already described above the condition of the trichiation in the wing of the Triassic fossil *Archipanorpa*, the only known representative of this Order.

It will be seen that this wing differs from all known Holometabola at present existing in having the archedictyon still present, upon all parts of the wing-membrane, in an aphantoneuric condition, and carrying macrotrichia upon it, mostly at the junctions of two or more venules.



Text-fig.21.*

Further, it should be noted that both macrotrichia and microtrichia are considerably larger in this fossil than in other Holometabola. The tendency towards reduction in size can be seen to be operating independently in all Orders; it culminates, in the case of the microtrichia, in their complete elimination from the wings of the higher families of the Planipennia and Lepidoptera; and, in the case of the macrotrichia, in a great reduction in their number and shortening in their length, in the case of the Diptera and certain Mecoptera.

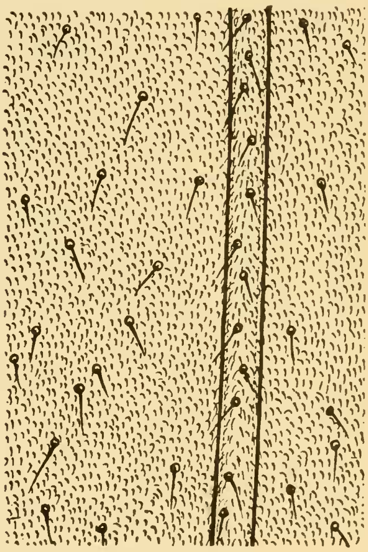
Order MEGALOPTERA. (Text-fig.22).

The most archaic members of this family exhibit a near approach, in arrangement of the trichiation, to that seen in the Protomecoptera. We have selected the genus *Archichauliodes* as

* Arrangement of the bases of insertion of the scales on a small portion of the wing of the Hawk-Moth *Cœquosa triangularis* Don., to show the pattern of the lost archedictyon; (× 50).

an illustration (Text-fig. 22); it belongs to the most archaic family *Corydalidæ*, of the Suborder Sialoidea.

The arrangement of the trichiation differs from that of *Archipanorpa* only in the complete loss of the archedictyon, and in the smaller size of both macrotrichia and microtrichia. As has been already pointed out, if the macrotrichia on any area of this wing be plotted out, they will still show, by their positions on the membrane, the pattern of the lost archedictyon. There is a well developed series of strong cross-veins supporting the main veins at wide intervals. None of these cross-veins carry macrotrichia. But the veinlets of the costal area and round the margin of the wing all show macrotrichia well developed.



Text-fig. 22.*

When we turn to the more specialised genera, we find a great advance over the condition seen in *Archichauliodes.* Take, for instance, the genus *Sialis*, of the family *Sialidæ*, Suborder Sialoidea. Here, although the microtrichia are still present abundantly all over the wing, yet the macrotrichia have quite disappeared, except round the fringe of the wing, and on the pterostigmatic area.

An advance in a different direction is to be seen in the Suborder Raphidioidea, of which the genus *Raphidia* will serve as an example. Here the microtrichia have completely disappeared, but the irregular thickening of the wing-membrane remains as

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* Portion of a main vein and surrounding membrane from the wing of *Archichauliodes guttiferus* Walk., to show the trichiation; (×100).

an indication of that disappearance. The macrotrichia have also disappeared from the membrane, but are still present on the veins. As a high specialisation, only to be paralleled in the highest families of the Planipennia, we note also that the macrotrichia appear for the first time upon the true cross-veins, thus rendering them indistinguishable from veinlets except by the fact that they are not preceded by tracheæ in the pupal wing.

We may sum up the tendency of evolution of the trichiation in this Order by saying that both macrotrichia and microtrichia appear to have been, from the very first, of small size; and that, although the most archaic genera still show the original arrangement of the trichiation, preserved almost in full, yet reduction set in very early, leading to the loss of one or other series of hairs in all the higher types of the Order.

The wing-trichiation of the Archetype of this Order will be taken to be similar to that of the archaic genus *Archichauliodes*, but with hairs of somewhat larger size.

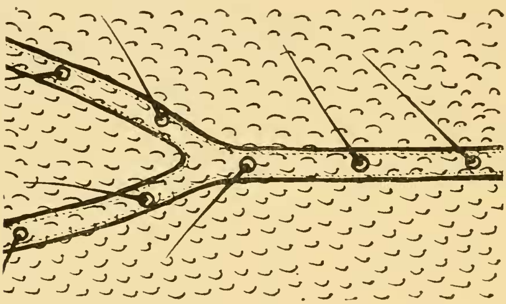
Order PLANIPENNIA. (Text-figs. 20, 23, 24).

The oldest known types of this Order show a wing-trichiation already specialised in certain directions. No traces of the archedictyon are to be found, and macrotrichia have, in every case, been eliminated from the membrane of the wing (Text-fig. 23). This is easily understood, when we remember that the wing-venation of the Order early underwent a unique specialisation, in the form of a rapid proliferation of sectors of the main veins, and especially of the branches of the radial sector. This produced the "Prohemerobiid" type (still to be seen in recent *Psychopsidæ*) in which the whole of the wing is covered with numerous parallel longitudinal veins, with few or no cross-veins supporting them. In the very narrow spaces between these veins, it was clearly impossible for the archedictyon to exist, and the macrotrichia upon it probably disappeared with it.

Starting, then, from a type having no macrotrichia upon the membrane of the wing, we find a further specialisation, in the higher families of this Order, in the complete elimination of the microtrichia. Thus we may divide the Order into two groups, as follows:—

(1). The more archaic families, with microtrichia still present. These are the *Ithonidæ*, *Hemerobiidæ*, *Dilaridæ*, *Sisyridæ*, *Coniopterygidæ*, *Psychopsidæ*, *Polystœchetidæ*, and *Osmylidæ*.

(2). The more specialised families, with microtrichia absent. These are the *Trichomatidæ*, *Berothidæ*, *Chrysopidæ*, *Apochrysidæ*, *Mantispidæ*, *Nymphidæ*, *Nemopteridæ*, *Myrmeleontidæ*, and *Ascalaphidæ*.

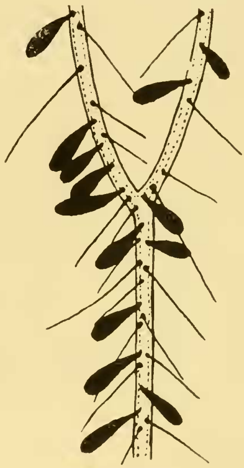


Text-fig.23.
Portion of a main vein and surrounding membrane from the wing of *Micromus tasmaniæ* Walk., to show the trichiation: (×200).

In the first group, macrotrichia are never found upon the true cross-veins. In the second, we find in the *Trichomatidæ* and *Berothidæ* forms showing the passage of the macrotrichia from the main veins on to the cross-veins. For instance, in the genus *Stenobiella*, the cross veins remain without macrotrichia, as in the first group. In *Spermophorella*, one or two isolated macrotrichia may be found upon most of the cross-veins. In *Trichoma*, there is an intense proliferation of macrotrichia upon the main veins; and they overflow, not only on to the cross-veins, but also, in some places, even on to the membrane itself. As this genus is evidently specialised in its excessive hairiness, there can be little doubt that this latter occurrence is in the nature of a cænogenetic development, and is not to be considered as an archaic survival of macrotrichia from an original archedictyon.

Apart from the two families dealt with in the preceding paragraph, all those listed in the second group have the macrotrichia well developed upon the cross-veins.

Another interesting specialisation in this Order is the development of *scales*, which occur in the family *Berothidæ*. They occur upon a more or less restricted area of the hindwing, in the females only, of the genus *Spermophorella* (Text-fig.24), and upon the fringe of the wing in the genus *Isoscelipteron*. They are clearly only modified macrotrichia.



Text-fig.24.*

The Archetype of this Order, then, may be defined as having had the archedictyon and its macrotrichia completely eliminated, owing to the unique specialisation of the venation: the macrotrichia, consequently, only occurring on the main veins and their branches, but well developed: and the microtrichia also present and of normal size. From this original type, the line of evolution runs forward in the direction of complete elimination of the microtrichia, with subsequent invasion of the cross-veins by the macrotrichia, and with the occasional formation of scales (in two cases only).

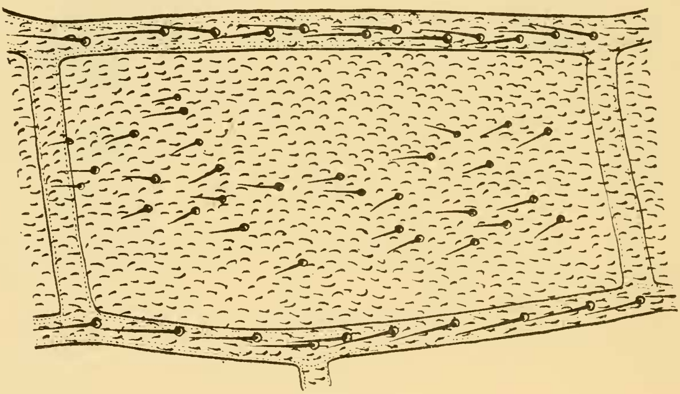
Order MECOPTERA. (Text-fig.25).

In this Order, microtrichia are always exceedingly well developed all over the wing. Macrotrichia are found upon the main veins and their branches, but never upon the true cross-veins. The archedictyon has been completely eliminated, but its macrotrichia still persist upon the wing-membrane. (Text-fig.25). Owing, however, to the small number of macrotrichia that can

* Portion of a main vein from middle of hindwing of *Spermophorella disseminata* Till., ♀, showing normal macrotrichia interspersed with seed-like scales; (×90).

be accommodated in the somewhat narrow spaces between the main veins, the original pattern of the archedictyon tends to become lost, and the macrotrichia of the membrane tend to become arranged in regular sets occupying the central part of any closed area of the wing.

The line of evolution in this Order is towards a gradual elimination of the macrotrichia from the membrane of the wing, and a reduction in their size elsewhere. In the most archaic families, such as *Meropidæ* (Text-fig.25) and *Choristidæ* (Plate lxix., fig.13), these hairs are still to be found upon the membrane, in almost every part of the wing. In the *Panorpidæ*, we may see the stages of gradual elimination from the basal areas of the



Text-fig.25.

A single areole from the wing of *Merope tuber* Newm., to show the trichiation; (×100). Note the absence of macrotrichia from the two cross-veins bounding the areole.

wing, while those left in the more distal areas become, for the most part, very regularly arranged in rows parallel to the main veins. In the *Nannochoristidæ*, we see a further stage of reduction reached, the macrotrichia being here entirely absent from the membrane of the hindwing; while, in the forewing, they only remain upon the anterior portion of the pterostigma. Finally, in the highly specialised *Bittacidæ*, all the macrotrichia have disappeared from the membrane, while those left upon the main veins have become short, stout spines, resembling those found in many Diptera.

As the true cross-veins are always weakly chitinised, and entirely free from macrotrichia in this Order, we have, in the macrotrichia, a valuable aid in the tracing out of the courses of the main veins. In many genera, the extreme base of Cu_1 is sharply bent up to join M not far from its origin, and so takes on the appearance of a cross-vein. But the true nature of this vein is still proclaimed by the presence of well-developed macrotrichia upon it.

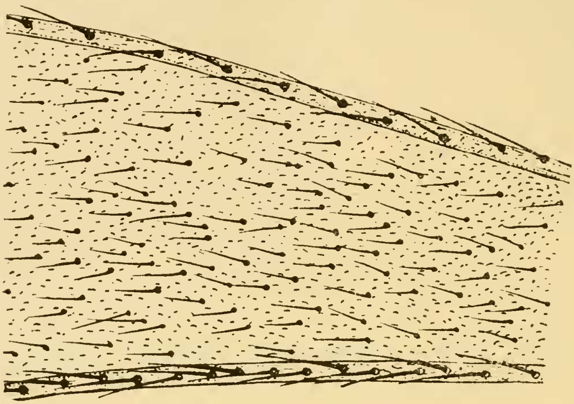
To sum up, then, we may characterise the Archetype of this Order as differing from that of the Protomecoptera only in the complete loss of the archedictyon. While the microtrichia remain constant throughout the course of evolution, the macrotrichia undergo a gradual reduction in size and number.

Order DIPTERA.

(Plate lxviii., fig.12; Plate lxix., fig.14, and Text-figs.26-29).

We take this Order next, since it appears to be, on the evidence of the wing-trichiation, a direct evolutionary derivative from the base of the Order Mecoptera.

Throughout the Order, microtrichia are present upon the wing. Macrotrichia are to be found upon the main veins and their branches; they tend to become reduced both in size and number. In only one family that I have examined are macrotrichia to be found upon the membrane, viz., in the *Rhyphidæ* (Plate lxviii., fig.12, and Text-fig.26). In this family, the structure and size of the macrotrichia are closely similar to those of the older Mecoptera. The arrangement of the macrotrichia upon the wing-membrane, however, shows the pattern of the archedictyon much more definitely than in any existing Mecopteron; so that, on this character, the *Rhyphidæ* can only be derived from a very early form of Mecopteron, if they are to be derived from that Order at all. In this connection, it is interesting to note that the family *Rhyphidæ* combines within itself characters of both the Nemocera and Brachycera. This accords well with the condition of the wing-trichiation; and the two characters taken together suggest that this family represents one of the most archaic types of Dipteron still existing.*



Text-fig.26.

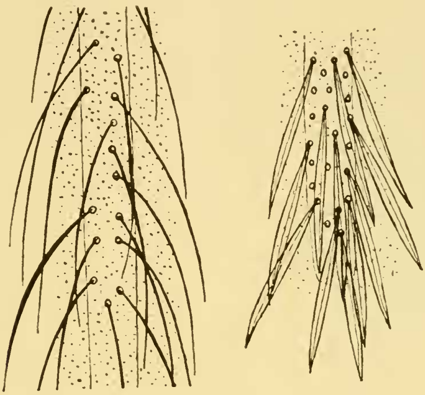
Portion of two main veins and the included membrane from the wing of *Rhyphus brevis* Walk., to show the trichiation; (× 130). (See also Plate lxviii., fig.12).

From the type of trichiation still existing in the *Rhyphidæ*, all other types to be found within the Order are derivable, by elimination of the macrotrichia from the wing-membrane. There are, however, two distinct lines of evolution to be traced, in one of which the macrotrichia tend to become slender and elongated, and finally develop into scales; while, in the other, they tend to become short and stout spines, and also become gradually eliminated from all except the anterior veins and costal border of the wing.

As conspicuous examples of the first line of evolution, we may take the Moth Midges or *Psychodidæ* (Text-fig.27). Here we see the macrotrichia as slender hairs abundantly present upon

* In this connection, it should be noted that the short vein usually considered as a cross-vein connecting Cu_1 with M_3 in *Rhyphus* is really the basal piece of M_4, since it carries macrotrichia. On the other hand, the vein below it, usually considered to be the basal portion of Cu_1, is a true cross-vein and carries no macrotrichia.

all the main veins and their branches. Here and there these hairs are seen to be slightly flattened out, forming delicate and narrowly lanceolate scales. The culmination of this same line of

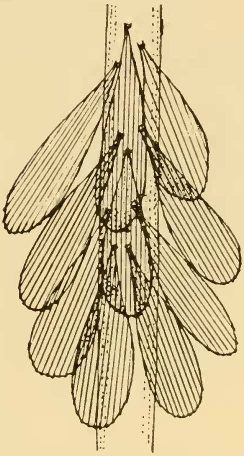


Text-fig.27.

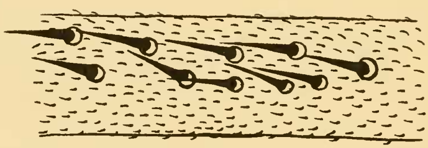
Two portions of a single main vein from the wing of *Psychoda* sp., (Hornsby, N.S.W.), to show the trichiation. On the left, normal macrotrichia, one or two slightly flattened; on the right (distal end of vein), narrow lanceolate scales; (× 375).

evolution is to be found in the *Culicidæ* (Text-fig.28), in which all the macrotrichia, even those along the wing-border, have become scales; and these scales, in most cases, are of broad form and specialised sculpture.

Along the second line of evolution, which has been followed by many families of Nemocera, and also by the whole series of the Brachycera and Cyclorrhapha, we can follow out the gradual elimination of the macrotrichia, through such forms as the *Tabanidæ*, where they are still present in large numbers on the more anterior veins of the wing, to the higher Cyclorrhapha, where they finally cease to exist anywhere except upon the costal border of the wing. Text-fig.29 shows the type of short, stiff seta into which the macrotrichia develop in this line of evolution. It should be noticed, also, that, concurrently with the broadening and strengthening of certain veins, the macrotrichia upon them become arranged two, three, or even four rows deep, so that the whole vein takes on a spiny appearance. Concurrently with this change in the macrotrichia, we find two lines of evolution of the microtrichia. They either undergo gradual reduction also, until they become partly or entirely eliminated, as in the family *Syrphidæ*; or they may remain well developed, with a differentiation setting in in the size of the two series on the upper and lower surfaces of the wing. In this latter case, the microtrichia on the *upper* surface increase considerably in size, while those of the lower surface remain fairly constant. This development takes place in the Myiodaria, and is especially well shown in the *Muscidæ*. In the Blowfly, for instance, the microtrichia of the upper surface of the wing are quite 30μ in length, and are set in large, swollen bases, while those of the lower surface are only about half as long, and have the usual small bases of insertion. (Plate lxix., fig.14).



Text-fig.28.*



Text-fig.29.
Small portion of a main vein from the wing of *Tabanus* sp., (Hornsby, N.S.W.), to show the trichiation; (× 200).

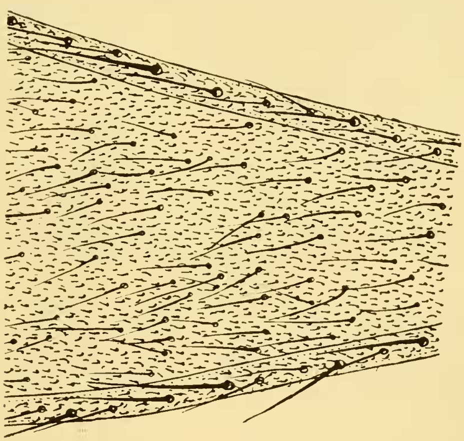
While, therefore, the main mass of the Diptera shows considerable specialisation in its wing-trichiation, we have to postulate

* Small portion of a main vein from the wing of a Mosquito, *Mucidus alternans* Westw., ♀, to show scales; (× 200).

for this Order, on account of the existence of the archaic *Rhyphidæ*, an Archetype similar to that of the Mecoptera, but with the microtrichia somewhat smaller than in that Order.

Order TRICHOPTERA. (Text-figs.30, 31).

In this Order, the most archaic types, such as the *Rhyacophilidæ*, already show considerable specialisation in their wing-trichiation. The archedictyon is always absent, but its macrotrichia are present upon the wing-membrane, and remain there, on the whole with ever increasing abundance, as we pass to the highest types within the Order. Microtrichia are present throughout the Order, but are always small, averaging about 5μ in length. Macrotrichia are present upon the main veins and their branches, but never upon the few and weakly developed cross-veins, except in the cases where the proliferation of these hairs upon the membrane leads to a secondary invasion of all parts of the wing.



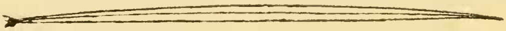
Text-fig.30.

Portion of two main veins and the included membrane from the wing of *Rhyacophila dorsalis* Curtis, to show the trichiation: (× 105). (Microtrichia are slightly exaggerated in this figure).

In describing the macrotrichia of the Protomecoptera, we have already mentioned that those found upon the archedictyon were somewhat smaller in size than those upon the veins. This difference is also to be seen, somewhat more intensified, in the older types of Trichoptera, as may be seen in the figure taken from *Rhyacophila dorsalis* (Text fig.30). Not only are the macrotrichia of the veins larger, but they remain for the most part straight and stiff, whereas those of the membrane (derived originally from the archedictyon), are slenderer, and inclined to be slightly curved.

A single line of evolution may be said to characterise the whole Order. It consists in the gradual greater and greater proliferation of the macrotrichia of the membrane, together with various specialisations of the macrotrichia upon the veins. Thus there is produced that excessively hairy type of wing that is especially associated with this Order. In many genera, the stiff bristles of the veins become reduced, either in part, or altogether, to the same type of slender flexible hairs that we find upon the membrane; in others, certain sets of hairs, especially at the base of the cubitus, become erect and bristly. In the *Hydroptilidæ*, all the macrotrichia of the forewings become erect and thickened, while the hindwing develops an exceedingly long fringe.

a



b

Text-fig.31.

Forms of scales found in Trichoptera : *a*, a narrow, lanceolate scale, with single longitudinal stria, from wing of an unnamed Leptocerid (Broken Hill, N.S.W.); (×350): *b*, a lanceolate scale with three longitudinal striæ from wing of *Plectrotarsus gravenhorsti* Kol.; (×400).

The slender, flexible macrotrichia of the membrane found in the wings of Trichoptera are exactly comparable with those of the *Psychodidæ* in the Order Diptera (Text-fig.27). Like them, they are easily converted into elongated lanceolate scales. The simplest type of such a scale is one in which the flattening produces only sufficient width to allow of the development of a single longitudinal stria (Text-fig.31,*a*). Such scales may be found in quite a number of isolated genera within the Order. Further broadening leads to the addition of a second, third, or even a fourth parallel stria. The best developed scales known to me in this Order are those of the peculiar genus *Plectrotarsus* (Text-fig. 31,*b*), which always show three or four striæ.

Certain groups of genera show a tendency to the reduction of the hairiness of the wings, which is evidently of a secondary nature. In the subfamily *Macronematinæ*, this culminates in the evolution of a number of forms with the wings almost devoid of macrotrichia.

In conclusion, the Archetype of this Order must evidently have had a wing-trichiation closely resembling that of *Rhyacophila*, *i.e.*, with the archedictyon absent, its macrotrichia present upon the membrane, and already differing considerably, in their smaller size, and slighter, more flexible build, from the larger and more bristle-like macrotrichia of the veins. Macrotrichia were absent from the cross-veins, and the microtrichia were already reduced to a small size.

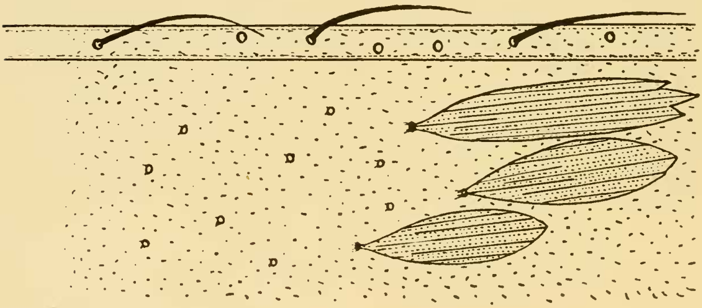
Order LEPIDOPTERA.

(Plate lxviii., fig.11, and Text-figs. 21, 32-34).

In this large Order, it will only be necessary to study fully the most archaic types; in the higher families, only the general trend of the evolutionary effort need be considered.

We take, then, first of all, the three families of the Suborder Homoneura, viz., the *Micropterygidæ*, *Prototheoridæ*, and *Hepialidæ*. In all of these, microtrichia are present, but exceedingly minute, never exceeding 2μ in length. They have been called *aculeæ* in this Order, and an attempt has been made to class together all those families, in which they occur, as the "Aculeate" Lepidoptera. They occur in a number of the older families of the Heteroneura, as well as in the Homoneura. Hence it will be seen that this method of classification is faulty, and should not be persisted in. In all the higher families, microtrichia are no longer present; but it is evident that their loss has been effected along many lines of advance; and that an association of all "non-aculeate" forms into one Suborder would be as unnatural a grouping as it would also be in the Order Planipennia.

The most striking character of the Order Lepidoptera is the specialisation of the macrotrichia as *scales*, throughout the whole Order, from the lowest to the highest forms. Although, as we have already seen, scales are to be found on the wings of other Orders of Holometabola (Planipennia, Diptera and Trichoptera), yet in each case they only occur spasmodically, as cases of high specialisation in one or more isolated groups. But, in the Lepidoptera, the scale-bearing habit is an ordinal character, the only exceptions to which can be traced definitely to retrogression (*e.g.*, in the *Psychidæ*).



Text-fig. 32.

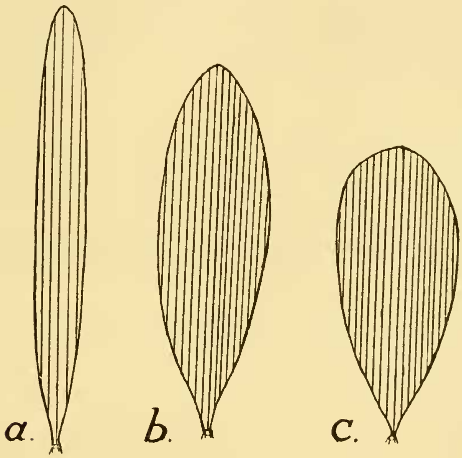
Small portion of a main vein and adjacent membrane from the forewing of *Prototheora petrosema* Meyr., (S. Africa), to show the trichiation; (× 200). (From a partially descaled specimen).

In order to establish the proof that these scales are modified macrotrichia, it is only necessary for us to study such an archaic type as *Prototheora** (Text-fig. 32), in which the macrotrichia upon the veins remain in their original state of somewhat flexible hairs, while the arrangement of the bases of insertion of the scales upon the membrane can be seen to correspond with the pattern of an original archedictyon. It will also be noticed that

* For the supply of material of this rare genus, I have to thank Dr. Péringuey, Director of the South African Museum, Capetown.

the scales that lie closest to the veins are elongate and narrow; and that, the further we go away from a vein, the broader and shorter the scales become. Thus we can find, in this one insect, all stages in the evolution of a scale from a macrotrichion present upon different parts of the wing.

Similar variations in the form of the scales, connected with their positions in relation to the veins, are to be found in the *Micropterygidæ* (Text-fig.33); but, in this family, the broader scales are much more abundant, and may frequently be seen quite close up to the veins.



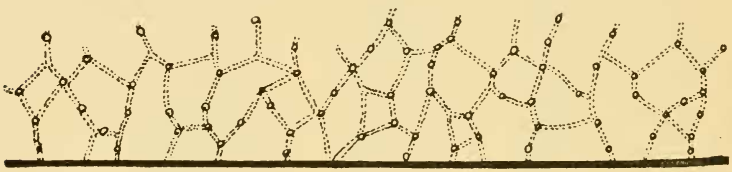
Text-fig.33.

Three types of scales found in the family *Micropterygidæ*; (× 400): *a*, from *Eriocrania semipurpurella* Steph.; *b*, from *Mnemonica subpurpurella* Haw.; *c*, from *Sabatinca incongruella* Walk. (All three types may be found upon any one genus).

In the *Hepialidæ*, both narrow, lanceolate scales and moderately broad, oval ones are scattered all over both membrane and veins, interspersed with fairly numerous, slender, flexible hairs, or macrotrichia which have remained unaltered in form.

It will not be necessary, for the purposes of this paper, to follow out the many specialisations to be found in the scales of the Heteroneura. These have already been very fully dealt with by many authors.

Returning to the *Prototheoridæ*, it is of the very greatest interest to note that traces of the original archedictyon are still to be found in this archaic family. In Text-fig.34, and Plate lxviii., fig.11, I show the very definite archedictyon that is to be seen above the radius. Here, not only do the macrotrichia (which, in this region of the wing, are all scales, not hairs) show very clearly the original arrangement of the meshwork, but there is actually a slight thickening and darkening of the membrane forming the archedictyon itself. Allowing for the difference in the sizes of the two wings, this condition in *Prototheora* is closely similar to that preserved in *Archipanorpa*. Though I have not



Text-fig.34.

Portion of the aphantoneuric archedictyon preserved above the radius of the forewing in *Prototheora petrosema* Meyr.; (× 130). (See also Plate lxviii., fig.11).

been able to find so good an example of an aphantoneuric archedictyon as this, anywhere else within the Order, yet there are numerous cases in which what appears to be the last remnant of the archedictyon can be seen in proximity to the veins, usually in the form of a series of slightly darkened and thickened spurs projecting almost at right angles to the main vein upon which they abut.

Reviewing the above evidence, it would seem that, in the Lepidoptera, the formation of scales must have begun before the complete disappearance of the archedictyon. This suggests that the scales in this Order must be an exceedingly archaic character, originating in a specialisation of some type belonging to an ancestral Order in which the archedictyon still persisted.

Hence we conclude that the Archetype of this interesting Order must have possessed at least some portions of the aphantoneuric archedictyon; that it also possessed microtrichia of small size; and that the macrotrichia, though remaining as slender, flexible hairs upon the veins, were largely interspersed with true scales upon the wing-membrane, such scales being of elongate, lanceolate form, with few striæ.

We have now to review the above evidence, in order to discover what light it throws upon the Phylogeny of the Orders included in the Panorpoid Complex.

First of all, it must be evident that, as far as the Wing-trichiation is concerned, all six Orders may well have been derived from a single ancestral Order characterised by the following points: presence of an aphantoneuric archedictyon, presence of microtrichia all over the wing, and presence of well-developed macrotrichia upon the main veins and their branches, and upon the archedictyon, but *not* upon the true cross-veins.

Such a type is preserved in the fossil *Archipanorpa* from the Trias of Ipswich, Queensland. This fossil itself, however, cannot have been the ancestral form, since the Mecoptera, Trichoptera, and Planipennia, at any rate, are contemporaneous with it, while the first of these three Orders goes back also into the Permian. For the actual ancestor we must postulate some unknown type of the Lower Permian, or possibly even of the Upper Carboniferous; and whether this ancestor is to be considered as belonging to the Protomecoptera or not, will have to depend upon other characters not dealt with in this Part.

Let us now follow the evolutionary changes of the various structures of the wing separately.

T h e A r c h e d i c t y o n :—This undergoes complete suppression in all recent Orders, except only in a few Lepidoptera, where distinct traces of the meshwork in an aphantoneuric condition (but not so well marked as in *Archipanorpa*) are still to be found. This is well shown above the radius in the forewing of *Prototheora petrosema* Meyr. (Text-fig.34, and Plate lxviii., fig.11).

After the elimination of the archedictyon, the bases of insertion of the macrotrichia left upon the membrane of the wing still show, fairly plainly, the original pattern of the lost meshwork. A study of the meshwork in the figures of *Prototheora* already referred to will soon convince us that it is possible to reconstruct the course of the meshwork with *fair* accuracy, by joining up the bases of the macrotrichia along the lines which they still indicate. The resulting figure will not be correct in all particulars, since some of the cross-venules of the mesh do not carry any macrotrichia at all, and would therefore be omitted in the reconstruction; while, in a few cases, the positions of the macrotrichia are more or less misleading.

In specialised cases where the macrotrichia proliferate freely on the veins and membrane, as in the case of the higher Heteroneurous Lepidoptera, there are always more than sufficient macrotrichia to ensure an accurate tracing of the original pattern of the archedictyon. This is well shown in the figures of the Hawk-Moth *Cæquosa triangularis* Don., (Text-fig.21). Here it will be seen that the meshwork, probably while it was still aphantoneuric, tended to become arranged into almost parallel lines connected by irregular cross-pieces. It is this tendency, carried to its highest development, that gives the very regular arrangement of the scales seen in the Butterflies. But in all cases, by careful study, it can be seen that the arrangement is a modification of an original meshwork, and not a series of unconnected straight lines.

The evidence afforded by the archaic *Rhyphus* in the Diptera, and by both the Homoneura and the older types of the Heteroneura in the Lepidoptera, points definitely to the conclusion that these two Orders, like the less highly specialised Orders of the Panorpoid Complex, had their macrotrichia arranged upon the membrane in the original positions which they occupied upon the aphantoneuric archedictyon.

The Microtrichia:—Though absent in the higher types of some Orders, *e.g.*, Megaloptera, Planipennia, Diptera (a few), and Lepidoptera (the great majority), yet they are found to be present upon the wings of archaic types of all the Orders of the Panorpoid Complex. The line of evolution is towards reduction in size in all the Orders, with the single exception of the Myiodaria in the Diptera, where there is an increase in size of the microtrichia upon the *upper* surface of the wing only, resulting in the interesting condition found in the Blowfly and allies (Plate lxix., fig.14).

The Macrotrichia:—A study of archaic types, including the fossil *Archipanorpa*, shows us that these were originally present upon both archedictyon and main veins, but not upon cross-veins. Moreover, probably because of the comparative weakness of the venules of the archedictyon, there was, from the very first, a considerable difference in size between the macrotrichia of the veins and those of the meshwork. The macrotrichia of the veins also tended to be more erect than those of the membrane; so that, in the fossil *Archipanorpa*, their bases of insertion show the two concentric circles of the raised disc very clearly, while those of the meshwork rarely do so.

We are thus led to expect the following lines of evolution, which do, in fact, actually take place in the various Orders of the Complex:—

(1) If the direction of the evolutionary effort be towards reduction, then the macrotrichia on the meshwork should be affected first, since they are smaller in size from the first, and inserted in less strongly built bases.

As a matter of fact, it will be seen that the tendency towards reduction in the smaller macrotrichia becomes accelerated in the course of evolution; so that, in many cases, they become quite eliminated, while the macrotrichia upon the veins may even proliferate, though usually undergoing some reduction in size as well, as in the higher Diptera.

(2) If the direction of the evolutionary effort be towards the formation of scales, then the macrotrichia of the meshwork should be affected first, since they are in a more favourable condition, both as regards their delicacy of structure and the condition of their bases of insertion, to undergo this change.

The formation of scales in the Lepidoptera and Trichoptera agrees with this; since, in archaic families of the former Order, and in all scale-bearing genera of the second, we can still find some at least of the macrotrichia on the main veins remaining in the form of hairs. Judging also from the tendency, in the Lepidoptera, for the broadest (most highly evolved) scales to appear furthest from the veins, while narrow lanceolate scales are found nearest to the veins, we are led to the same conclusion. Actually, the covering of scales is not needed so much upon the veins as upon the membrane, and the original condition of the macrotrichia is such that the need of the insect is to be met along the easiest line of specialisation; *i.e.*, those macrotrichia whose alteration into scales would most benefit the insect also happen to be those in the best condition to undergo the change.

In the other Orders in which scales appear (Diptera, Planipennia) it should be noticed that they are a comparatively late effort, which takes place after the macrotrichia have been completely eliminated from the membrane of the wing. The scales, in these cases, are formed from the macrotrichia left on the veins. If these are still somewhat bristly, as in the Planipennia, a hard, seed-like scale is produced (Text-fig. 24); if, however, they have become slender and delicate, as in the *Psychodidæ* and *Culicidæ*, then the resulting scales will resemble very closely those of the Lepidoptera and Trichoptera.

The changes in position of the macrotrichia, in connection with the disappearance of the archedictyon, have been already dealt with above.

Taking all the above evidence into account, we may reasonably come to the following conclusions, as far as the limitations of this Part of our study permit:—

(1) The fossil Order Protomecoptera is undoubtedly the most archaic type known within the Panorpoid Complex, as regards the characters of its Wing-trichiation.

(2) A single line of descent from the Protomecoptera to the Mecoptera, and from the very base of this latter Order to the Diptera, is strongly indicated by the uniform type of trichiation

found in these three Orders, together with the very definite evolutionary trend towards reduction.

(3) A second line of descent is less definitely indicated, comprising the Megaloptera and Planipennia, in which the evolutionary tendency runs towards early complete suppression of the macrotrichia upon the membrane of the wing, and a later invasion of the macrotrichia from the main veins on to the cross-veins, culminating in the Raphidioidea on the one hand, and in the higher Planipennia on the other. Both Orders may well have been derived from an early type of Protomecopteron, but neither of them can be derived from the other. For the oldest Planipennia have the largest microtrichia, while the oldest Megaloptera still retain the macrotrichia upon the membrane, a condition which is not to be found within the Planipennia.

(4) As the Trichoptera show a more archaic condition of the macrotrichia upon the membrane than do most of the Mecoptera, they can only be derived either from the very base of this latter Order, or from the preceding Protomecopterous type.

(5) In the Lepidoptera there exist certain types that show portion of the archedictyon still present in an aphantoneuric condition: while, in many others, the pattern of the archedictyon is well preserved. Both the oldest Trichoptera and the oldest Mecoptera are in advance of these types. Hence we can only trace back the Lepidoptera to the Protomecopterous or some similar, extinct type, and may not derive them either from the Mecoptera or from the Trichoptera.

Though the conclusions to be drawn from the structures studied in this Part are somewhat indefinite in themselves, they will be found to be of considerable value when taken in conjunction with the rest of the evidence. Also, in the study of the Phylogenies of the families of each separate Order, (which lies outside the actual scope of this paper), a great deal of very valuable evidence may be gathered from the Wing-trichiation.

We may conclude this Part by giving, in tabular form, the principal characters of the Wing-trichiation for the different Orders—

TABLE OF THE CONDITION OF THE WING-TRICHIATION IN THE ORDERS OF THE PANORPOID COMPLEX.

* indicates well-developed, × present in reduced form, – absent.

Orders and Groups.	Micro-trichia.	Macrotrichia. On main veins and branches.	Macrotrichia. On cross-veins.	Macrotrichia. On arche-dictyon or membrane.	Arche-dictyon.
PROTOMECOPTERA ...	*	*	–	*	present, aphanto-neuric.
MEGALOPTERA :—					
Archetype	*	*	–	*	–
Corydalidæ	*	*	–	*	–
Sialidæ	*	–	–	(A)	–
Raphidiidæ	–	*	*	–	–
PLANIPENNIA :—					
Archetype	*	*	–	–	–
Archaic types ...	* or ×	*	–	–	–
Higher types ...	–	(B)	*	–	–
MECOPTERA :—					
Archetype	*	*	–	*	–
Archaic types ...	*	*	–	* or ×	–
Nannochoristidæ and *Bittacidæ*	*	*	–	(C)	–
DIPTERA :—					
Archetype	*	*	–	*	–
Rhyphidæ	*	*	–	*	–
Psychodidæ	×	some scales	–	–	–
Culicidæ	×	all scales	–	–	–
Other types... ...	*, × or –, (D)	* or ×	–	–	–
TRICHOPTERA :—					
Archetype	×	*	–	*	–
Recent families ...	×	*	(E)	very abundant, sometimes scales. (F)	–
LEPIDOPTERA :—					
Archetype	×	*	–	hairs and scales	at least partially present, aphanto-neuric.
Prototheoridæ ...	×	* (hairs and scales)	–	scales	partially present, aphanto-neuric.
Other Homoneura ...	×	,,	–	hairs and scales	–
Archaic Heteroneura	×	,,	–	,,	–
Higher Heteroneura	–	scales	–	scales	–

Special References:—(A) Only present on fringe and pterostigma—(B) Some scales developed on hindwing of *Spermophorella* ♀♀ and fringe of *Isoscelipteron*—(C) A few present on pterostigma of forewing in *Nannochoristidæ*—(D) Absent in some *Syrphidæ*; enlarged on upper surface of wing in Myiodaria—(E) Absent except as a late invasion from the membrane—(F) Sparse or absent in *Macronematinæ* and some other forms.

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(*Note.*—The reference-numbers are made consecutive from Part to Part, but only those referred to in any given Part are printed with that Part).

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EXPLANATION OF PLATES LVII.-LXIX.

Plate lxvii.

Fig.9.—Portion of forewing of the fossil *Archipanorpa magnifica* Till., showing the aphantoneuric archedictyon with tubercles representing the bases of insertion of the macrotrichia; also showing portion of the main veins R_3 and R_4, with clearly marked bases of insertion of larger macrotrichia, and cross-veins without the same; (×27).

Fig.10.—Part of Fig.9, further enlarged; (×43).

Plate lxviii.

Fig.11.—Portion of forewing of *Prototheora petrosema* Meyr., (Lepidoptera; S. Africa), showing the radius, with the aphantoneuric archedictyon above it, carrying scales (macrotrichia); from a cleared mount of a partially de-scaled specimen; (×50).

Fig.12.—Portion of forewing of *Rhyphus brevis* Walker (Diptera), showing distribution of microtrichia and macrotrichia; most of the latter have become detached from their bases of insertion; (×400).

Plate lxix.

Fig.13.—Apical portion of forewing of *Chorista australis* Klug, (Mecoptera), showing distribution of microtrichia and macrotrichia; notice the absence of the latter from the cross-veins; (×200).

Fig.14.—Portion of forewing of Blowfly (*Calliphora villosa* Desv.; Diptera), showing the two types of microtrichia; the larger ones are on the upper, the smaller on the undersurface of the wing; (×60).

(All figures are from photomicrographs, Figs.9-10 from the actual fossil, Figs.11-14 from cleared mounts of wings).